Characterization and classification of mycorrhizae of Douglas-fir. III. *Pseudotsuga menziesii* + *Byssoporia* (*Poria*) *terrestris* vars. *lilacinorosea*, *parksii*, and *sublutea*

B. ZAK[1]

Forestry Sciences Laboratory, Pacific Northwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, Corvallis, OR, U.S.A. 97331

AND

M. J. LARSEN

Center for Forest Mycology Research, Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, P.O. Box 5130, Madison, WI, U.S.A. 53705[2]

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Three distinct Douglas-fir (*Pseudotsuga menziesii*) ectomycorrhizae formed by newly recognized varieties of *Byssoporia* (*Poria*) *terrestris* are described. They are named according to tree species and fungus as follows: *P. menziesii* + *B. terrestris* var. *lilacinorosea*, *P. menziesii* + *B. terrestris* var. *parksii*, and *P. menziesii* + *B. terrestris* var. *sublutea*. Each mycorrhiza is macroscopically and microscopically defined, including surrounding mycelium and attached rhizomorphs. Cultural characteristics of the three fungal symbionts grown on potato dextrose agar medium are briefly noted.

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Les auteurs décrivent, chez le sapin de Douglas (*Pseudotsuga menziesii*), trois ectomycorhizes distinctes formées par des variétés récemment découvertes de *Byssoporia* (*Poria*) terrestris. Les mycorhizes sont nommées d'après l'espèce d'arbre et de champignon, comme suit: *P. menziesii* + *B. terrestris* var. *lilacinorosea*, *P. menziesii* + *B. terrestris* var. *parksii*, et *P. menziesii* + *B. terrestris* var. *sublutea*. Chaque mycorhize, y compris le mycélium avoisinant et les rhizomorphes, est définie macroscopiquement et microscopiquement. Les caractères culturaux des trois symbiontes fongiques, cultivés sur un milieu gélosé de dextrose et pomme de terre, sont brièvement notés.

[Traduit par le journal]

Introduction

Zak (1969*a*) described two distinct Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) mycorrhizae from western Oregon formed by different strains of *Byssoporia* (*Poria*) *terrestris* (DC. ex Fries) Larsen & Zak,[3] a blue-staining strain and an orange-staining strain. These strains have been renamed as *Byssoporia* vars. *sartoryi* and *aurantiaca*, respectively, and the mycorrhizae are now designated as *P. menziesii* + *B. terrestris* var. *sartoryi* and *P. menziesii* + *B. terrestris* var. *aurantiaca*.

Described here are three additional Douglas-fir ectomycorrhizae from western Oregon, each formed by a variety of *B. terrestris*. The mycorrhizal designations are *P. menziesii* + *B. terrestris* var. *lilacinorosea* Larsen & Zak, *P. menziesii* + *B. terrestris* var. *parksii* (Murr.) Larsen & Zak, and *P. menziesii* + *B. terrestris* var. *sublutea* Larsen & Zak. Fungal symbionts of the first two were briefly referred to earlier by Zak (1969*b*, 1971, 1973) as *P. terrestris* (rose-staining) and *P. terrestris* (yellow), respectively.

Methods

Fungal symbionts of the three mycorrhizae were identified by linking their fungal tissues with tissues of the respective associated sporocarps according to the procedure outlined by Zak (1971, 1973). Attached mycelia and rhizomorphs were carefully examined macroscopically and microscopically. Ultraviolet (UV) light (3600 Å (1 Å = 0.1 nm)) fluorescence and chemical reagent color reactions (Singer 1962) of tissues were determined. Isolates of the fungi obtained from respective mycorrhizae and sporocarps were cultured on nutrient agar media and the resulting growth was rigorously compared. Except for *P. menziesii* + *Byssoporia terrestris* var. *sublutea*, identification of each mycorrhiza was based on at least three separate mycor-

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[1]Present address: P.O. Box 867, Kalaheo, HI, U.S.A. 96741.

[2]Maintained in cooperation with the University of Wisconsin, Madison, WI, U.S.A.

[3]In a separate paper, we propose the new genus ***Byssoporia*** to accommodate *P. terrestris* and its varieties (Larsen and Zak 1978).

rhiza–sporocarp collections. Well developed mycorrhizae, however, were synthesized with *B. terrestris* var. *sublutea* in pure culture; syntheses with vars. *lilacinorosea* and *parksii* were not attempted. Color designations are based on Munsell Book of Color (1966).

Fungi were isolated in pure culture according to the following schedule. Selected, initially clean, 2- to 5-mm pieces of mycorrhiza elements or 5- to 10-mm lengths of rhizomorphs were agitated with a needle loop, two or three at a time, in a 60 × 15 mm petri dish of 30% H_2O_2 for 5–20 s. A 2- to 5-min rinse in a 100 × 20 mm petri dish of sterile water followed immediately. The pieces were then placed on potato dextrose agar medium (PDA), as formulated by Lacy and Bridgmon (1962), or on Melin-Norkrans medium (MMN) as modified by Marx (1969).

Anatomical sections were prepared by fixing mycorrhiza elements in CRAF (Johansen 1940), embedding in paraffin, and microtoming 8–12 μm thick. Sections were stained with safranin followed by fast green.

Pseudotsuga menziesii + *Byssoporia terrestris* var. *lilacinorosea*

Macroscopic Characters (× 10)

Mature mycorrhiza in regular pinnate fans (Fig. 1), simple, compound, or double compound, up to 1.5 cm broad and 0.5–2 cm long, occurring singly, or when in clusters up to 3 cm diam; individual elements strongly tortuous, uniformly (0.4–)0.5(–0.7) mm diam; young mantle brightly white with or without faint pink tinges, finally becoming dull white without staining or gross color change; surfaces of young mycorrhizae and attached concolorous rhizomorphs finely granular; mycorrhizal elements interconnected by loose fine white mycelium and hyphal strands attached to thread-like rhizomorphs up to 0.2 mm diam and more than 10 cm long; older mycorrhizae with surrounding mycelium collapsed with rhizomorphs appearing attached directly; mantle fluorescence in UV moderately strong dull pinkish white to dull rose or coral; chemical reagent color reactions of mantle: chlorovanillin, pink to red within 5 min; 15% KOH, immediately turning brown, sides and exposed cut surfaces of elements becoming maroon after 1 min; sulfoformol, scraped mantle fragments become pale yellow in 1 min; guaicol, phenol, formaldehyde, alphanapthol, pyrogallol, concentrated H_2SO_4, and Melzer's reagent (for formula see Slysh (1960)) provided erratic or no observable reactions.

Microscopic Characters (× 100–400)

Mycorrhizal surface a loose tangle of characteristic septate, thin-walled, lightly encrusted staghorn hyphae (1–)2(–2.7) μm diam; mantle prosenchyma 15–40 μm thick with the outer half of interwoven septate, thin-walled hyphae 2–4.5 μm diam and the inner half of septate, thin-walled hyphae 1.5–4.5 μm diameter formed in stellate patterns; Hartig net well developed, one hyphal diameter of 2–3 μm thick (Fig. 2).

Loose mycelium surrounding mycorrhizal elements moderately to heavily encrusted with amorphous deposits which disappear in saturated chloral hydrate and in 5% KOH; in saturated chloral hydrate, hyphae thin walled, septate, opaque and hyaline, (1–)1.5(–2.5) μm diam, hyphal fusions infrequent, clamps absent.

Core hyphae of rhizomorphs (Fig. 3) closely packed, straight, parallel (sheathed by a thin layer of narrow entwining hyphae), thin walled, septate, single and pair branched, (2.5–)3.5(–8) μm diam, with few hyphal fusions and few to many clamps; entwining sheath hyphae moderately to heavily encrusted, thin walled, septate, single branched, (1.5–)2.5(–3) μm diam, with frequent hyphal fusions and few to many clamps; hyphal strands similar to rhizomorphs but core and sheath hyphae (2–)2.5–3(–4) μm diam, and staghorn hyphae infrequent.

Isolation and Culture of Fungus

Byssoporia terrestris var. *lilacinorosea* was readily isolated in pure culture from surface-sterilized mycorrhizal elements and from surface-sterilized pieces of rhizomorphs. On PDA, it forms a raised, slow-growing mat (Fig. 4), brightly white at first becoming a weak, dull rose after 1 month.

Habitat, Distribution, and Occurrence

Mycorrhizal collections were made in second-growth and virgin Douglas-fir stands in the Coast Ranges near Corvallis, Oregon, at elevations of 300–700 m. All specimens were found in brown-rotted wood debris partially buried in the soil; none were observed in the humus layer or in mineral soil. The mycorrhiza appears in early November, several weeks after the beginning of fall rains, and can be found throughout the winter months until spring. Although not investigated, the fungus probably also forms mycorrhizae with western hemlock and grand fir scattered through these forests. Distribution of the mycorrhiza is not known, but it likely occurs throughout the Pacific Northwest.

Other mycorrhizae commonly associated with this form on Douglas-fir roots include those of *Cenococcum geophilum* Fr. (=*C. graniforme* (Sow.) Ferd. & Winge), *Rhizopogon vinicolor* Smith, *Piloderma bicolor* (Pk.) Jülich (=*Corticium bicolor* Pk.), and two or three unidentified fungi. Occasionally a silver-lavender mycorrhiza formed by *Cortinarius* sp. also occurs with this mycorrhiza.

Distinguishing Features

The diagnostic characteristics that permit separation of var. *lilacinorosea* are the white mycor-

rhizal mantle free of staining, tortuous elements, presence and character of surrounding mycelium and rhizomorphs, fine granular covering of mantle, mycelial, and rhizomorph surfaces, and UV fluorescence and chemical reagent color reactions of the mantle. The staghorn hyphae associated with the mantle and especially rhizomorph surfaces are particularly notable. Sporocarps of the fungal symbiont are first brightly white but when older acquire rose to dull to bright red stains. This variety is grossly similar to *Pseudotsuga menziesii* + *Byssoporia terrestris* var. *sartoryi* (Zak 1969*a*).

Pseudotsuga menziesii + *Byssoporia terrestris* var. *parksii*

Macroscopic Characters (× 10)

Mature mycorrhizae in racemose to irregular pinnate fans (Fig. 5), up to 1.5 × 2 cm, simple and compound, individual elements tortuous, uniformly (0.4–)0.6(–0.8) mm diam; mantle pale greenish yellow (near 7.5Y; 8.5/10) with rusty orange stains along elements; surface finely crusty with sparse overlying loose greenish yellow mycelium resembling algal filaments; threadlike rhizomorphs up to 0.2 mm diam and 5 cm long, smooth to finely crusty, attached to mantle at first dull greenish yellow and later rusty orange; UV fluorescence of mantle moderately strong; dull yellowish olive and 1- to 2-mm element tips dull orange; young rhizomorphs fluoresce moderately strong dull yellowish olive, while older ones fluoresce orange; chemical reagent color reactions: concentrated NH_4OH, within $\frac{1}{2}$ min turns mantle, attached rhizomorphs, and surrounding mycelium bright orange and surrounding liquid pale yellow; 15% KOH, similar to concentrated NH_4OH but orange duller; guaicol, phenol, formaldehyde, chlorovanillin, alphanapthol, pyrogallol, concentrated H_2SO_4, and Melzer's reagent provided erratic or no observable reactions.

Microscopic Characters (× 100–400)

Anatomy typically ectomycorrhizal; mantle (15–)25(–35) μm thick, with a uniform prosenchyma of tightly interwoven hyphae (2–)3(–4) μm diam and heavily encrusted surface hyphae; Hartig net well developed, one hyphal diameter of 1.5–3 μm thick (Fig. 6).

Hyphae of surrounding mycelium heavily to moderately encrusted, fairly straight, (1.5–)2(–2.6) μm diam, few to many hyphal fusions with or without center septum, clamps few to absent; after 1–2 weeks in Hoyer's mounting medium (Anderson 1954), hyphal surfaces appear spiculated, covered with scattered spherical deposits, or many hyphae densely coated with needlelike crystals 1–1½ hyphal diameters long and aligned mostly across width of hyphae.

Rhizomorphs (Fig. 7) with a core of broad, closely packed, straight, parallel, hyaline hyphae sheathed by thin layer of narrow entwining hyphae which in older rhizomorphs give rise to an appressed, heavily encrusted surface lattice; core hyphae encrusted only in smaller rhizomorphs, (4–)5–8(–11) μm diam, thin walled, septate with few to many clamps, single and pair branched, hyphal fusions few and without septa, sheath hyphae 2.5–3.5 μm diam, thin walled, septate, single branched, many hyphal fusions; surface lattice hyphae of larger rhizomorphs thin walled, septate, 1.5–5.5 μm diam; hyphal strands extending from rhizomorphs have similar core and sheath hyphae but with core hyphae (3.5–)4.5(–8) μm diam.

Encrustations golden-yellow to orange in mass, highly refractive in phase illumination, partially to mostly dissolved in Hoyer's mounting medium, saturated chloral hydrate, and 5% KOH.

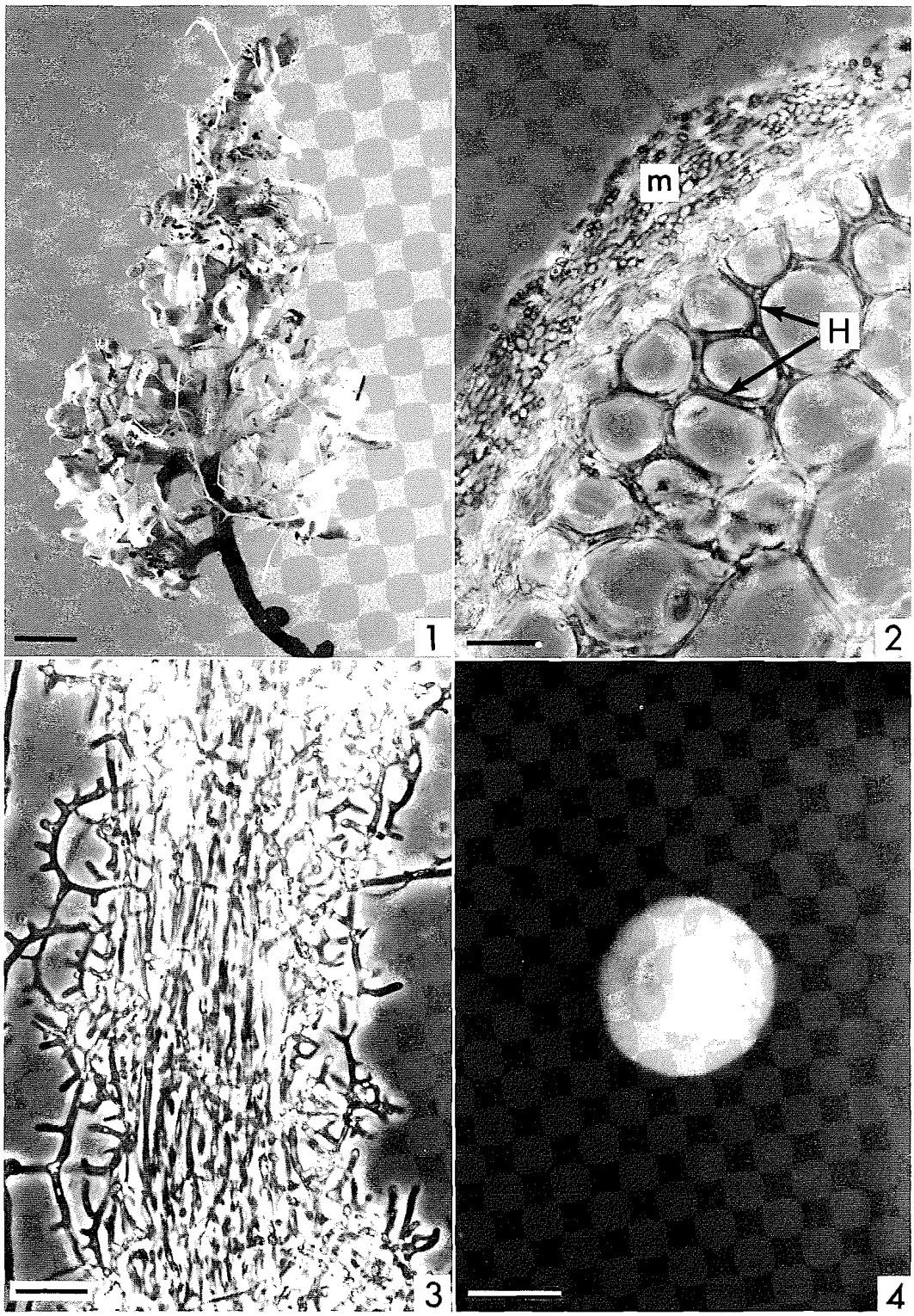
Isolation and Culture of Fungus

Byssoporia terrestris var. *parksii* grows very slowly on PDA and MMN and is, therefore, more difficult to isolate. Surface-sterilized pieces from rhizomorphs attached to sporocarps and mycorrhizae yielded only 5% isolation success. On PDA, the mat (Fig. 8) is first raised, white to very pale yellow-green, later becoming rather appressed, coarsely felty, white to cream with tan and dark grey-brown zones; underside a uniform dark brown.

Habitat, Distribution, and Occurrence

This mycorrhiza has been found in mineral soil and in mineral soil mixed with decayed wood fragments directly beneath decayed wood debris. Sporocarps associated with the mycorrhizae, how-

FIGS. 1–4. *Pseudotsuga menziesii* + *Byssoporia terrestris* var. *lilacinorosea*. Fig. 1. Cluster of young pinnate mycorrhizae. Scale line equals 2 mm. Fig. 2. Freezing microtome cross section of fresh mycorrhiza cut 25 μm thick, mounted in Hoyer's medium, and viewed by phase-contrast lighting. Scale line equals 20 μm. Fig. 3. Rhizomorph attached to mycorrhiza; note staghorn surface hyphae. Mounted in 5% potassium hydroxide and viewed by phase-contrast lighting. Scale line equals 20 μm. Fig. 4. Forty-day-old mat of *B. terrestris* var. *lilacinorosea* grown on potato dextrose agar medium at 20°C in the dark. Scale line equals 1 cm.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ever, usually occur in the overlying decayed wood adjacent to the soil. Collections have been made only in second-growth Douglas-fir stands, at elevations of 300–700 m, in the Coast Ranges near Corvallis, Oregon. As with the other *Byssoporia terrestris* mycorrhizae in this region, they appear shortly after the beginning of fall rains in late October or early November and persist until early spring.

No other collections of this mycorrhiza or of mycorrhizae of other tree species formed by *Byssoporia terrestris* var. *parksii* are known, but sporocarps of the fungus have been reported from Banff National Park in Canada, Glacier National Park in Colorado, Arizona, and Georgia associated, respectively, with *Pseudotsuga menziesii*, *Picea* spp., *Pinus ponderosa* Laws., and *Pinus taeda* L., with which the fungus presumably is mycorrhizal (Larsen and Zak 1978).

Mycorrhizae commonly associated with *Pseudotsuga menziesii* + *Byssoporia terrestris* var. *parksii* include those formed by *Cenococcum geophilum* and several other unidentified ones.

Distinguishing Features

This variety may be recognized by the green-tinted yellow mycorrhizal mantle with finely encrusted surfaces, the macroscopic character of rhizomorphs, the superficial resemblance of surrounding mycelium to algal filaments, color of UV fluorescence, and chemical reagent color reactions. Usually, the characteristic sporocarps of the fungal symbiont are associated with the mycorrhiza. At first, the sporocarps are uniformly pale yellow (near 7.5Y; 9/6), later becoming deep yellow (near 5Y; 8.5/12) with occasional orange stains.

Pseudotsuga menziesii + *Byssoporia terrestris* var. *sublutea*

Macroscopic Characters (× 10)

Mature mycorrhizae in irregular open pinnate to regular closed pinnate fans (Fig. 9), up to 1.5 cm broad, 2 cm long, simple, compound, or double compound, occurring singly or in clusters up to 3 cm diam; individual elements tortuous to straight, (4–)5(–7) mm diam; surface of mantle powdery, at first sulfur yellow (near 5Y; 8/10), later pale coral or pale pinkish cream (near 5YR; 8/6) with a somewhat tomentose surface; abundant rhizomorphs attached directly to mantle, threadlike, up to 1.0 mm thick, 10 cm long, appearing concolorous and powdery surfaced; UV fluorescence of young mantle and rhizomorphs deep maroon (near 2.5R; 4/14); chemical reagent color reactions: 95% ethyl alcohol, young mantle immediately turns dull white, a pink tint evident from underlying tissue; concentrated H_2SO_4, immediately bright reddish-orange which decolorizes after a few minutes; 15% KOH, immediately bright orange but quickly changing to dull reddish orange; concentrated NH_4OH, immediately bright reddish orange and then quickly fading; erratic or no observable reactions in chlorovanillin, $FeSO_4$, guaicol, Melzer's reagent, pyrogallol, sulfobenzaldehyde, and sulfovanillin.

Microscopic Characters (× 100–400)

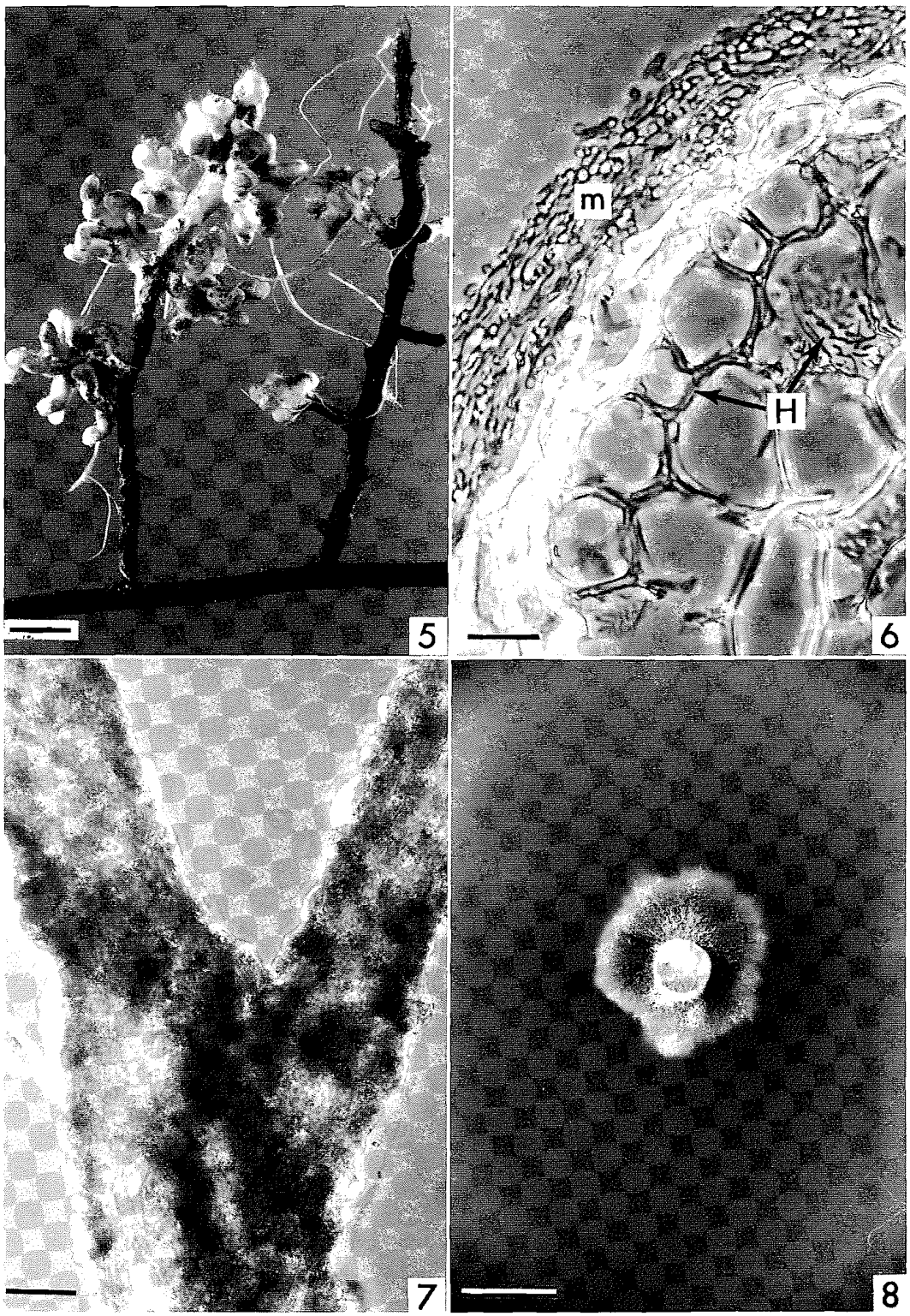
Anatomy typically ectomycorrhizal (Fig. 10); mantle surface a loose tangle of heavily encrusted, thin-walled, uniform septate hyphae 1.5–2 μm diam, many hyphae characteristically spiral or corkscrewlike, clamps absent; mantle (15–)25(–40) μm thick, with a fairly uniform prosenchyma of tightly interwoven hyphae (1.5–)2.5–3(–5) μm diam; Hartig net well formed, 1 hyphal diameter of 1.5–2 μm thick.

Hyphae of surrounding mycelium sparse, heavily to moderately encrusted, consisting of fairly straight, thin-walled, septate hyphae (1.5–)2(–3) μm diam; clamps infrequent; these hyphae giving rise to associated hyphae of smaller diameter loosely arranged, similar to mantle surface hyphae but with spiral shape more accentuated (Fig. 13).

Rhizomorphs (Figs. 11, 12) with a core of broad, thin-walled, hyaline irregular hyphae, (4–)8(–13) μm diam, closely packed and parallel, clamps infrequent with single and pair branching; sheath hyphae uniform in outline, (2–)4(–6) μm diam, clamped and with few hyphal fusions; spiral-shaped surface hyphae arising from mantle surface, byssoid, similar to those of the mantle surface; sheath and surface hyphae moderately to heavily encrusted; hyphal strands similar but with core hyphae of a smaller diameter and fewer surface hyphae.

Encrustations on mycorrhizae and associated mycelium dull yellow in mass, highly refractive in phase-contrast illumination, and largely disappearing in 95% ETOH, 15% KOH, saturated chloral

FIGS. 5–8. *Pseudotsuga menziesii* + *Byssoporia terrestris* var. *parksii*. Fig. 5. Young mycorrhizae. Scale line equals 2 mm. Fig. 6. Freezing microtome cross section of fresh mycorrhiza cut 25 μm thick, mounted in Hoyer's medium, and viewed by phase-contrast lighting. Scale line equals 20 μm. Fig. 7. Rhizomorph attached to mycorrhiza mounted in Hoyer's medium and viewed by phase-contrast lighting. Scale line equals 20 μm. Fig. 8. Forty-day-old mat of *B. terrestris* var. *parksii* on potato dextrose agar medium at 20°C in the dark. Scale line equals 1 cm.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hydrate, and Hoyer's mounting medium, leaving the walls appearing finely spiculed.

Isolation and Culture of Fungus

Variety *sublutea* grows somewhat faster than varieties *sartoryi*, *aurantiaca*, *lilacinorosea*, and *parksii* on PDA and MMN and is readily isolated in pure culture. Isolation success from H_2O_2 surface-sterilized pieces of rhizomorphs attached to sporocarps and to mycorrhizae was about 20%. On PDA, the mat (Fig. 14) is raised, the center two-thirds is lemon yellow, the margin is brightly white, later becoming pale to moderately dark tan with radiating depression lines; underside is a drab maroon.

Habitat, Distribution, and Occurrence

Byssoporia terrestris var. *sublutea* was first collected by J.M. Trappe in a subtropical *Quercus* forest in the state of Morelos, Mexico. Sporocarps were observed on old leaves and on decayed wood; connected rhizomorphs extended to clusters of *Quercus* mycorrhizae.

The characterization of *Pseudotsuga menziesii* + *Byssoporia terrestris* var. *sublutea* here outlined is based on only a single collection which represents the second find of this variety. An extensive pocket of mycorrhizae together with numerous sporocarps of the fungus was found in early November 1973 in an old-growth *P. menziesii*, *Tsuga heterophylla* (Raf.) Sarg., and *Thuja plicata* Donn stand on the western slope of the Cascade Range near Cascadia, Oregon, at an elevation of about 350 m. Both mycorrhizae and sporocarps were in brown-rotted wood partially buried in the soil and in underlying mineral soil containing fragments of decayed wood.

Only two other Douglas-fir mycorrhizae were found closely associated with this form. One was the ubiquitous black mycorrhiza formed by *Cenococcum geophilum*. The other was the white pinnate mycorrhiza of *Byssoporia terrestris* var. *sartoryi*; sporocarps of this fungus were also present. Although rather uncommon, the close association of Douglas-fir mycorrhizae formed by two different varieties of *Byssoporia terrestris* has been occasionally observed. Mycorrhizae of var. *sartoryi* were also found fairly common in the surrounding area, within 200 m of the collection site. Sporocarps, but not mycorrhizae, of var. *parksii* were noted in one nearby mass of decayed wood.

Distinguishing Features

This mycorrhiza may be separated from others similar to it by the powdery, sulfur yellow surface of the mantle, presence of concolorous rhizomorphs with the same surface texture as the mantle, lack of abundant surrounding mycelium, color of UV fluorescence of mantle and rhizomorphs, chemical reagent color reactions of mantle, association of distinctive sporocarps with a dull cream spore surface (10YR; 9/2) which becomes pale coral (7.5YR; 9/2) and the subiculum dull yellow (2.5Y; 8.5/6), and also, the notable spiralling characteristic of surface hyphae of mantle and rhizomorphs and of mycelium surrounding mycorrhizal elements.

Discussion

Like the two initially reported *Byssoporia terrestris* mycorrhizas of Douglas-fir formed by vars. *sartoryi* and *aurantiaca*, the three new *B. terrestris* mycorrhizae described in this paper are distinguished rather easily in the field by use of a 10 × hand lens. Features such as color and surface character of the mantle, abundance and character of mycelium and rhizomorphs surrounding elements, and gross form of the mycorrhiza permit identification of the five forms. Additionally, the characteristic sporophores of each variety of the fungus are usually found with their respective mycorrhiza.

Lowe (1966) lists *Byssoporia terrestris* from several areas of the United States and from Europe. Although largely limiting our collecting to western Oregon, we feel that varieties *sartoryi*, *aurantiaca*, *lilacinorosea*, *parksii*, and *sublutea*, ranked according to decreasing relative frequency, are widespread in Pacific Northwest coniferous forests. They are abundant in this region. For example, of 33 decayed Douglas-fir stumps examined in a 2-ha area in a second-growth Douglas fir stand near Cor-

FIGS. 9–14. *Pseudotsuga menziesii* + *Byssoporia terrestris* var. *sublutea*. Fig. 9. Cluster of mycorrhizae; note thick rhizomorph (arrow). Scale line equals 2 mm. Fig. 10. Cross section of paraffin-embedded mycorrhiza cut 12 μm thick and viewed by transmitted light. Scale line equals 20 μm. Fig. 11. Rhizomorph attached to mycorrhiza; note spiral surface hyphae. Mounted in 5% potassium hydroxide and viewed by phase-contrast lighting. Scale line equals 20 μm. Fig. 12. Cross section of paraffin-embedded rhizomorph cut 12 μm thick. Viewed by transmitted light. Scale line equals 20 μm. Fig. 13. Mycelium surrounding mycorrhizal elements; note spiral hyphae. Mounted in 5% potassium hydroxide and viewed by phase-contrast lighting. Scale line equals 20 μm. Fig. 14. Forty-day-old mat of *B. terrestris* var. *sublutea* grown on potato dextrose agar medium at 20°C in the dark. Scale line equals 1 cm.


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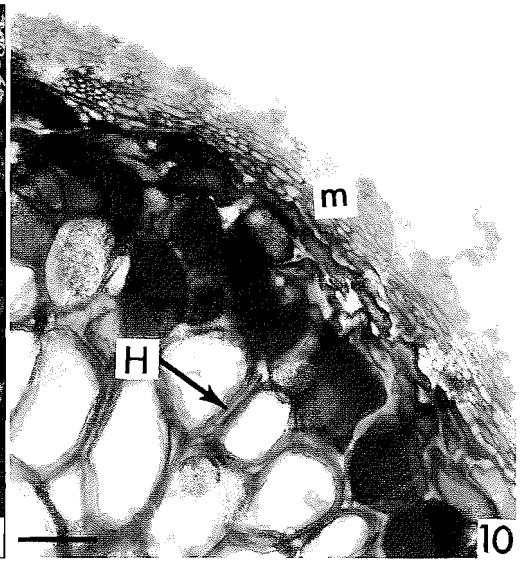
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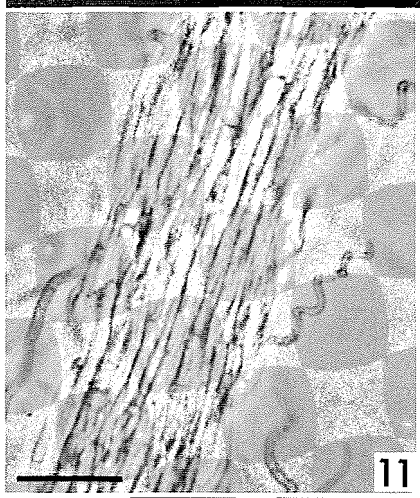
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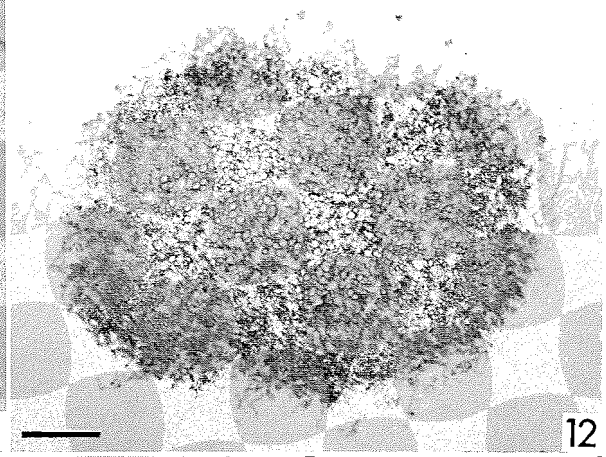
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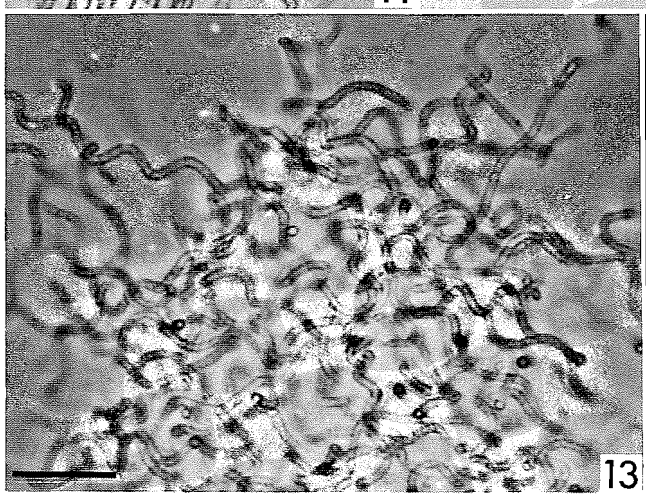
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vallis, Oregon, 26 contained sporocarps and mycorrhizae of var. *aurantiaca*, and two of var. *sartoryi* (Zak 1969*b*).

Additional varieties of *Byssoporia terrestris* and their associated mycorrhizae may be found, especially in other regions of North America and in Europe. Recently, one of us (Zak) discovered a white pinnate *Tsuga heterophylla* mycorrhiza along the Oregon coast, formed by what appears to be yet another variety of *B. terrestris*. Sporocarps are white without staining, and on PDA, the fungus grows differently than the other five varieties.

Acknowledgment

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